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VISUAL AND ACOUSTIC COMMUNICATION IN THE BRAZILIAN TORRENT FROG, *HYLODES ASPER* (ANURA: LEPTODACTYLIDAE)

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ABSTRACT: We studied the signaling, territorial, and courtship behaviors of the diurnal frog *Hylodes asper*. Visual and acoustic communication were used during intraspecific interactions involving males, females, and subadults. *Hylodes asper* has a complex visual communication system, of which foot-flagging is the most distinctive display observed in the repertoire of visual signals. The splash zone produced by the waterfalls and torrents creates a high, nearly constant, humidity near the streams, reducing the risk of desiccation which enables the diurnal activity of *H. asper*. Although the ambient sound pressure levels (SPL), measured at the calling sites, are similar to the SPL of the advertisement calls, the high-pitched calls of *H. asper* are spectrally different from the noise produced by the water current. Thus, the ambient noise produced by the water current may not interfere significantly with the acoustic communication of this species. The noise and the nearly constant and high humidity produced by the torrents and waterfalls, along with the availability of light, probably favored the evolution of contrasting colors and visual communication in *H. asper*. Males of *H. asper* excavate underwater chambers that are probably used to shelter the eggs and to prevent the clutch from being drifted downstream.

Key words: *Hylodes asper*; Anura; Hylodinae; Visual communication; Acoustic communication; Reproductive mode; Atlantic Forest; Southeastern Brazil

AMONG amphibians, vocalization is highly developed in anurans, most species of which have vocal structures capable of producing a variety of sounds that attract mates, advertise territories, or express distress (Duellman and Trueb, 1986). Communication by acoustic signals is effective in several circumstances, including situations where vision is limited (Gerhardt, 1983). Acoustic communication must have been favored by the pump breathing mechanism (Duellman and Trueb, 1986) and by the nocturnal activity observed for the majority of anuran species. The evolution of visual communication in some species of frogs has apparently been fa-

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vored by the availability of ambient light (Lindquist and Hetherington, 1996, and references therein). Diurnal species of anurans commonly use visual displays, apparently for communication (e.g., Durant and Dole, 1975; Wells, 1980), with limb signals being the most distinctive behavior described (e.g., Davison, 1984; Harding, 1982; Heyer et al., 1990; Pombal et al., 1994). The apparent use of limb signals for visual communication in anurans has been observed for the following genera: *Brachycephalus* (Brachycephalidae), *Atelopus* (Bufonidae), *Dendrobates* (Dendrobatidae), *Litoria* (Hylidae), *Hylodes* (Leptodactylidae), *Taudactylus* (Myobatrachydae), and *Staurois* (Ranidae) (see revision in Lindquist and Hetherington, 1996). In addition to these genera, leg signals are performed by males during territorial interactions in two nocturnal species in the genus *Phyllomedusa* (Hylidae) (*P. distincta:* Castanho, 1994; *P. burmeisteri:* observations by C. F. B. Haddad).

The subfamily Hylodinae comprises frogs distributed among the genera *Crossodactylus, Hylodes,* and *Megaelosia.* A great number of species in this subfamily is diurnal, and males of most species in the genera *Crossodactylus* and *Hylodes* have loud bird-like voices (Vielliard and Cardoso, 1996; Weygoldt and Carvalho e Silva, 1992); *Megaelosia* is apparently voiceless (Giaretta et al., 1993). Although some species of Hylodinae are common along small forest streams in south and southeastern Brazil, little is known about their reproductive behavior (Heyer et al., 1990; Weygoldt and Carvalho e Silva, 1992). *Hylodes asper,* which has a distribution from south to southeastern Brazil, occurring from Santa Catarina to Rio de Janeiro (Frost, 1985), is known for displaying both acoustic signals and apparent visual signals near mountain streams (Heyer et al., 1990; Hödl et al., 1997). In the present study, we describe the signaling, territorial, nest building, and courtship behaviors of this diurnal frog.

MATERIALS AND METHODS

The behaviors of *H. asper* were studied during 18 visits, totaling 45 days and 112 h of observations, from March 1988–March 1994, from 0530–2000 h. The study was conducted at Paranapiacaba, Município de Santo André (23°47′S, 46°18′W, 800 m above sea level), and Picinguaba, Município de Ubatuba (23°23′S, 44°50′W, 50–100 m above sea level), State of São Paulo, Brazil, in streams with waterfalls and extensive rapids.

Focal animal and all occurrence samplings were used for behavioral records (Lehner, 1979). Experimental manipulations were restricted to the manual insertion of a mirror (15 × 10 cm) next to resident males, to test the importance of vision during the territorial interactions. Descriptions of the behaviors are based on individuals observed and videotaped in the field. Individuals were not marked, but some of them were recognized in successive days by distinctive natural markings and color patterns. We recorded advertisement calls in a Nagra E tape recorder using a Sennheiser ME 80 microphone; other vocalizations were recorded in a Sony TCM-74v tape recorder using a Sony cardioid microphone. The sonograms were produced in a Macintosh computer coupled to the MacRecorder Sound System 2.0.5, using 8 bit resolution, 22 kHz sampling frequency, and FFT with 256 points. For the statistical analysis of the results, we used the Mann-Whitney rank sum test, with $\alpha = 0.05$ (Zar, 1996).

RESULTS

Hylodes asper was acoustically active in all months, showing a peak in activity during the rainy season (October–March). During the night, males, females, and juveniles of *H. asper* were observed resting in crevices or on branches and leaves up to 1.0 m above the ground, near streams. Tadpoles were observed performing feeding activities during the day and at night in the streams. Males started to emit advertisement calls during sunrise and stopped during sunset. The communication of *H. asper* is based on visual and acoustic signals, as described below.

Visual Communication Performed by Isolated Males

During the day, males defended emerged rocks and logs as territories, used

FIG. 1.—Territorial male of *Hylodes asper* performing foot-flagging display and emitting advertisement call. Note the inflated vocal sacs.

as calling and courtship sites, and for feeding activities. Males of *H. asper* observed from above are cryptically colored, resembling the dark substrate of their calling sites. However, when the male is observed from the front, in the plane that he might be observed by conspecifics, the white venter and bright vocal pouches contrast with the dark substrate, probably enhancing the visibility of the male. Some visual signals are associated with stereotyped behaviors that allow the exposure of the usually concealed contrasting colored parts. The most distinctive visual signal is the movement of a hind limb, which is generally displayed while calling (foot-flagging). When the male starts to call, he may raise one hind limb and extend it up and back in an arc-shape movement of approximately 45° from the substrate, maintaining the body stationary. When the leg is extended (Fig. 1) the toes separate and the silvery color of the dorsal surfaces of toes and toe fringes become visible. The leg returns to the male's side just after finishing the call, and during 1–2 s he wiggles the toes of both feet without moving the legs, showing the silver coloration (see similar descriptions in Heyer et al., 1990; Hödl et al., 1997). The movements of the silvery parts of the foot contrast sharply with the dark coloration of the male's body and with the dark substrate. Females of *H. asper* do not present this contrasting color pattern on the feet and were not observed performing foot-flagging.

We quantified the foot-flagging behavior of 11 calling males and observed that both left and right legs are used with similar frequencies (the right leg was used 71 times and the left leg was used 89 times); however, they were not used with regular alternation. The males may call without any observable movement of the limbs (*n* = 58 calls for 11 observed males). Sometimes the foot-flagging display (26 observations for eight males) and the movements of the toes (27 observations for two males) were performed by males that were not calling. We observed subtle, but apparently deliberate, up-and-down movements of one of the arms in front of the white chest, for two isolated males.

Territoriality and Visual Communication Performed by Interacting Males

At sunrise, males start to emit territorial calls (described below) near the nocturnal shelters, approximately 2–6 m from the calling site. At sunset, the males again emit territorial calls while returning to the nocturnal shelters. During the day, territorial males usually climb the rocks and logs near waterfalls and the fastest torrents to watch the territory and signal from an elevated position. Males call from these sites and consequently vocalizations are emitted from the noisiest parts of the streams. Males may return to the same calling site in successive days (*n* = 8 males) and may use the same nocturnal shelter for more than a month (*n* = 1 male). Females apparently do not defend territories; however, they were observed returning to the same diurnal sites in successive days (*n* = 4 females). Territorial males of *H. asper* were observed attracting females and actively hunting invertebrates inside the territories. Males seem to have an acute visual sense of movements; we observed males moving 3 m, by jumping on rocks and logs, to prey on small insects and spiders. After ingestion, the male returned to the calling site. When a territorial male perceives an intruder by sight or by hearing the advertisement call (described below), he increases the rate of advertisement calls and foot-flagging behavior.

We observed eight territorial interac-

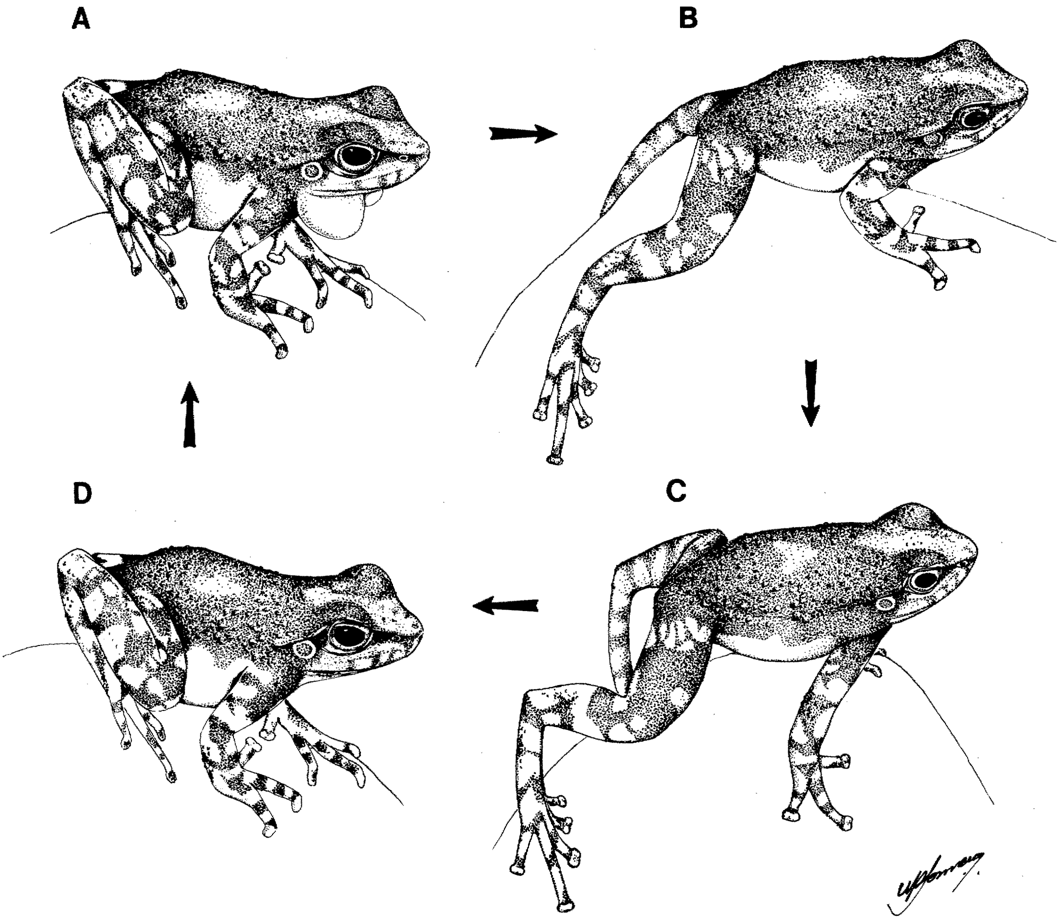

FIG. 2.—Territorial male of *Hylodes asper* (A) emitting territorial calls, (B) stretching the legs backwards, (C) lifting the body, and (D) prior to the emission of vocalization.

tions that finished before fights, eight that culminated in fights between two males, and one that culminated in a fight among three males. The interactions that finished before fighting involved males that were passing through areas already defended by resident males. In these cases, the intruders were pursued. During the pursuit, the territorial male begins emitting advertisement calls plus foot-flagging, and chases the intruder by using these behaviors as well as territorial calls. Sometimes during pursuit, the territorial male emits territorial calls plus the behavior of stretching the legs backwards at ground level and, subsequently, lifting the body (n = 6; Fig. 2); the intruder is chased until the frontiers of the territory. Fights may last for a few seconds to more than 1 h ($\bar{x}$ = 26.5 min, SD = 36.6, range 3 s to 85 min, n = 5) and may be subdivided into rounds ($\bar{x}$ = 2.5 rounds per fight, SD = 1.9, range 1–5, n = 4). When two males interact for the possession of a territory, the progression can be described as follows: one or both males start to emit advertisement calls with foot-flagging; then one or both males start to emit territorial calls with subtle up-and-down movements of one of the arms in front of the white chest (n = 1); then one or both males start to emit the territorial calls with the behavior of stretching the legs backwards without raising and, subsequently, lifting the body (n = 7). One male jumps, and using its snout, tries to beat against the rival; the other male tries to repel the attack by kicking the jumping male. The males fight by trying to enter between their rival and the substrate; the lower male attempts to dislodge the upper male by pushing him with the feet, arms, flanks, or dorsal surfaces of its head and body; the round is finished when one of the males is thrown down into the stream (the loser may return for another round) or when one of the males flees.

We observed seven territorial interactions between a subadult and an adult male of *H. asper*. Five interactions finished before fights and two culminated in fights between a male and a subadult. The territorial behaviors observed during these interactions involving an adult male and a subadult were similar to those described above for territorial males, except that the subadults were never observed emitting vocalizations or performing the foot-flagging behavior. However, subadults may show the behavior of stretching the legs backwards at ground level and, subsequently, lifting the body ($n = 4$; Fig. 2).

To test the importance of vision during the territorial interactions, we introduced a mirror into the territories of eight calling males. Just two males continued calling after this manipulation. One male did not change his behavior and continued to call; the other male stopped the advertisement calls, faced the mirror, started to emit territorial calls, stretched the legs backwards without raising and, subsequently, lifted the body (Fig. 2), then jumped against the mirror three times beating with the snout.

Diving Behavior of Males

In October 1993, we observed a male diving several times into the torrent and entering an underwater chamber. The male was excavating the chamber by removing the sand amidst some submerged rocks. The chamber was 20 cm in total length and its opening was 6 cm wide and was 17 cm below the water surface. The average time spent by the male underwater was 256 s (SD = 91, range 162–468 s, $n = 17$) and the mean interval between dives was 546 s (SD = 397, range 240–1230 s, $n = 10$). Sometimes, between dives, the male emitted advertisement calls and territorial calls. The activities performed by the male inside the chamber were not observed. After observation the chamber was inspected and contained no eggs.

Visual Communication and Courtship Behavior

We observed a total of 13 females being courted by males. In nine cases, females refused the males by fleeing during the courtship ritual. Courtship can be described as follows. When the male perceives an approaching female, he faces her and starts to emit the advertisement calls plus foot-flagging displays; the female signals acceptance by stretching one or both legs backwards at ground level (similar to the male in Fig. 2B) and performing subtle up-and-down movements of one of the arms in front of the white chest; the male and the female approach each other; the male emits a low intensity courtship call and then touches the female's snout with his gular region; the male jumps among the rocks and logs apparently attracting the female with advertisement calls and foot-flagging displays; the male then dives into the flowing water, followed by the female. One female consecutively repeated these behaviors with three different males, staying underwater for a few seconds with each one. Underwater behaviors were not observed. One dissected female contained several unpigmented oviductal eggs ($\bar{x}$ = 2.58 mm diameter, SD = 0.27, range 2.3–3.18, $n = 10$). One male of *H. asper* apparently signaled to a female of *Hylodes phyllodes* that was crossing his territory; the female did not respond to the male.

Vocalizations

Males likely call to attract females and to defend territories. Four different vocalization types were observed. The most common is the advertisement call that consists of high-pitched whistled trills. At an air temperature of 24–25 C, the advertisement calls are composed of 33–46 notes ($\bar{x}$ = 41.1, SD = 4.4, $n = 10$). The mean duration of this vocalization is 2.22 s (SD = 0.37, range 1.65–2.73, $n = 10$) and the mean duration of the notes is 27

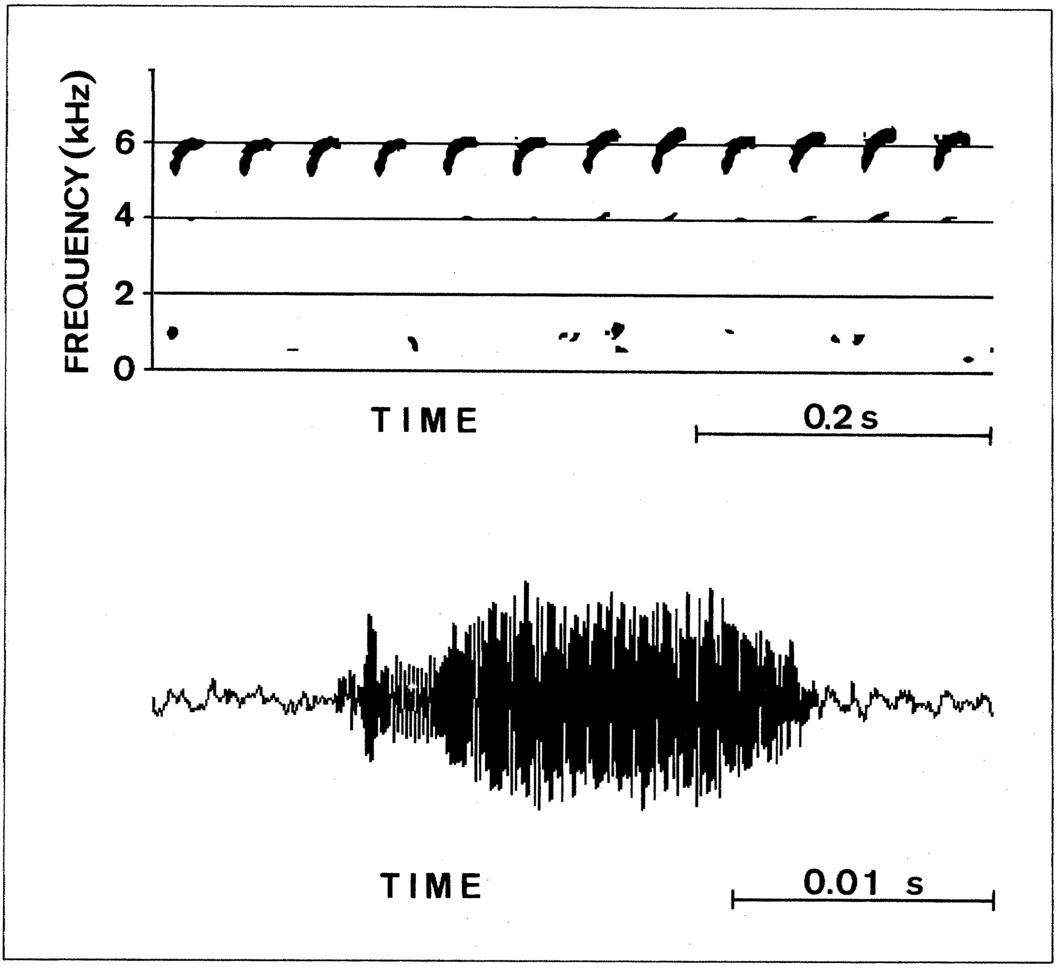

FIG. 3.—Sonogram (upper) of part of the advertisement call and wave form (lower) of one note of the advertisement call of *Hylodes asper*; the wave form corresponds to the last note in the sonogram. The ambient noise produced by the torrents is mainly 0–2 kHz. Picinguaba, Ubatuba, São Paulo; air temperature was 24–25 C.

ms (SD = 4, range 20–30, n = 36). Each note is an ascending frequency-modulated sound with the energy concentrated on the third harmonic, between approximately 5 and 6.5 kHz; the energy on the fundamental and second harmonic is low (Fig. 3). The fundamental, around 2 kHz, is not visible in the sonogram, and the second harmonic can be seen by weak marks around 4 kHz. The frequencies on the third harmonic are higher than the frequencies of the background noise produced by the torrents and waterfalls (Fig. 3). The intervals between advertisement calls emitted by males of *H. asper* that were not performing foot-flagging behavior ($\bar{x}$ = 88.7 s, SD = 58.1, range 44–313, n = 46 vocalizations of five males) were significantly higher ($P < 0.0001$) than the intervals between advertisement calls of males that were performing foot-flagging ($\bar{x}$ = 47.9 s, SD = 8.9, range 35–67, n = 26 vocalizations of two males).

Two vocalization types were emitted during agonistic male-male interactions: the territorial calls and squeals (Fig. 4). The territorial call is a note with a mean duration of 31 ms (SD = 6, range 20–40, n = 10), that is a frequency-modulated peep with the energy distributed in three

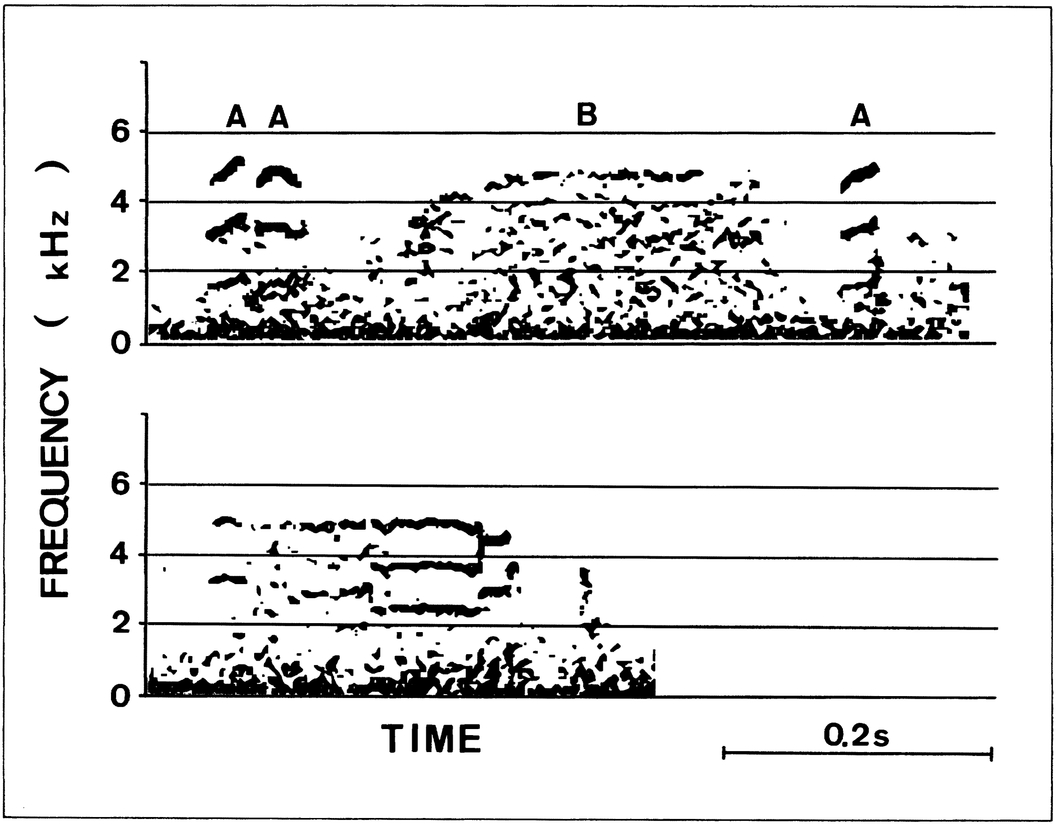

FIG. 4.—Sonograms of vocalizations emitted during agonistic male–male interactions of *Hylodes asper*: (upper) "A" notes are territorial calls and "B" note is a squeal without harmonic structure; (lower) squeal with harmonic structure. The ambient noise produced by the torrents is mainly 0–2 kHz. Paranapiacaba, Santo André, São Paulo; air temperature was 24–25 C.

harmonic structures between 1.4 and 5.6 kHz (Fig. 4 upper). Squeals emitted during fighting were variable in duration ($\bar{x}$ = 260 ms, SD = 90, range 170–460, *n* = 8) and structure; some squeals show harmonic structures (Fig. 4 lower) and in others the harmonics are not evident (Fig. 4 upper). The fourth vocalization type is a short, low intensity courtship call (not tape recorded), emitted when the male is close to the female during courtship.

DISCUSSION

Variable aggressive calls, as observed for *H. asper*, have been described for other frog species (e.g., Cardoso and Haddad, 1984; Wells, 1988) and may signal the motivational state of the opponents during agonistic encounters, helping to avoid the risks of physical combats (Martins et al., 1998). The lower intervals between advertisement calls of males of *H. asper* that were performing foot-flagging suggest that males that are calling and performing the foot-flagging behavior are more excited than males that are just calling. The advertisement call of *H. asper* is similar to the advertisement calls of several species in the genus *Hylodes* that, like *H. asper*, occur near torrents (e.g., Haddad et al., 1996; Heyer and Cocroft, 1986; Vielliard and Cardoso, 1996). The characteristics of the advertisement calls of some studied species in the genus *Hylodes* may be summarized as follows: short and numerous notes with harmonic structures and rapid raise and decay; energy concentrated on the third harmonic that is free from the low noise frequencies of the environment; notes rhythmically spaced within the sequences that are separated by long periods of silence. These characteristics have an adaptive significance in allowing the vocal signals to be heard in environments of high ambient water noise, facilitating the localization of the calling male (Dubois and Martens, 1984; Haddad et al., 1996; Vielliard and Cardoso, 1996).

Similar and convergent acoustic characteristics may be observed between frogs and birds from torrents and waterfalls of the Atlantic Forest mountains of Brazil (Vielliard and Cardoso, 1996) and of the Himalayan Mountains (Dubois and Martens, 1984). This general pattern of convergence among unrelated groups in different regions of the world demonstrates the effects of noisy environments on modeling the acoustic communication in animals. Although the ambient sound pressure levels (SPL), measured at the calling sites, are similar to the SPL of the advertisement calls (Hödl et al., 1997), the high-pitched calls of *H. asper* are spectrally different from the noise produced by the water current. Thus, the ambient noise produced by the water current may not interfere significantly with the acoustic communication of this species.

Species of anurans living near rain forest torrents and waterfalls are subject to a nearly constant, high relative humidity as a result of the waterfall splash zone. Therefore, these species are not subject to desiccation and could evolve a diurnal activity pattern. The noise produced by torrents along with the availability of light for the diurnal species of torrent frogs may have favored the evolution of contrasting colors and visual communication. The visual display and exposure of the contrasting colors might conceivably attract predators, but a frog on the edge of a mountain stream can easily escape from a predator by jumping into the swift waters (Heyer et al., 1990; Hödl et al., 1997; personal observations).

Torrent frogs of the genus *Staurois*, *Taudactylus*, and *Hylodes* display foot signals, apparently for visual communication in a convergent way (Harding, 1982; Heyer et al., 1990; Winter and MacDonald, 1986; present study). However, males, females, and subadults of *H. asper* have a complex system of visual communication, being foot-flagging behavior just one of the displays observed in the repertoire of visual signals of this species. Males of *Atelopus zeteki*, a montane stream species from Panama, perform visual communication using a subtle but apparently deliberate foot-raising behavior that is somewhat different from the foot-flagging display; besides this behavior, males of this species display a stereotyped forelimb waving signal (Lindquist and Hetherington, 1996). *Brachycephalus ephippium* was considered a diurnal forelimb signaling anuran, occurring in stream microhabitats (Lindquist and Hetherington, 1996); however, this species has direct development (Pombal et al., 1994) and is more common in quiet and humid places of the forest floor far from water bodies (personal observations). Consequently, the evolution of visual communication in *B. ephippium* apparently was not related to the constraints of the noisy environments of torrents and waterfalls, but may have been related to the diurnal activity and aposematic coloration of this species (Pombal et al., 1994). In the cases of *Litoria* and *Phyllomedusa*, which are nocturnal species, it is more difficult to understand the selective pressures leading to the evolution of visual communication. Species in both genera have contrasting color patterns on the hind limbs, which is apparently used in nocturnal visual communication among territorial males (*Litoria:* Heyer et al., 1990; Richards and James, 1992; *Phyllomedusa:* Castanho, 1994; observations by C. F. B. Haddad).

In the rheophilic subfamily Hylodinae, all known species of *Megaelosia* are apparently mute (Giaretta et al., 1993), some species of *Hylodes* are mute (Heyer, 1982) or have a weak vocalization and bright colors (Gouvêa, 1979), and *Crossodactylus gaudichaudii* displays apparent visual signals during territorial interactions (Weygoldt and Carvalho e Silva, 1992). These observations and characteristics are indicative that visual displays may be widespread among the species in this subfamily.

We can tentatively reconstruct the courtship behavior of *H. asper* as follows: the male excavates an underwater chamber near his calling site; he calls from emerged rocks and logs near torrent streams and near his chamber; a gravid female approaches the male, attracted by his acoustic and visual displays; after physical contact, the male guides the female to the underwater chamber; the female inspects the chamber and may accept or refuse to reproduce with the male; the female may engage with another male to inspect his chamber. In species in which the males construct nests for reproduction, the nest quality may be used by the females as a way to select males, which may be refused or accepted on the basis of the construction characteristics (e.g., *Hyla faber:* Martins, 1993; *H. leucopygia:* observations by C. F. B. Haddad).

The reproductive modes in the subfamily Hylodinae are not well known; only for two species, one in the genus *Crossodactylus* and another in the genus *Hylodes*, has the reproductive mode been identified. In both cases, males excavate underwater oviposition nests in the substrate of mountain streams (Faria et al., 1993; Weygoldt and Carvalho e Silva, 1992). Mutual touches between male and female engaged in courtship and/or the behavior displayed by the male of guiding the female to the oviposition site are typical of anuran species in which the male constructs a concealed nest for the clutch, before the arrival of the female (e.g., *Hyla leucopygia:* Haddad and Sazima, 1992; observations by C. F. B. Haddad; *Leptodactylus fuscus:* Martins, 1988). *Hylodes phyllodes* shows a courtship behavior similar to that observed for *H. asper:* the male touches the snout of his mate with the gular region; the female follows the male to the underwater nest (Faria et al., 1993). The unpigmented eggs observed in the dissected female of *H. asper* are indirect evidence that the clutch is deposited in places protected from insolation. The observation that males of *H. asper* excavate underwater chambers strongly suggests that the reproductive mode of this species is characterized by eggs deposited inside the chamber as a protection against predators and to prevent the eggs from drifting downstream; subsequently, feeding tadpoles abandon the chamber and go into the stream. This reproductive mode is uncommon among anurans and has only been observed for some Hylodinae frogs (Faria et al., 1993; Weygoldt and Carvalho e Silva, 1992; present study).

RESUMO

Os comportamentos de sinalização, territorial e de corte foram estudados para o anuro diurno *Hylodes asper*, com base nos sistemas de comunicação acústica e visual. Estes sistemas de comunicação são usados durante interações intraespecíficas envolvendo machos, fêmeas e subadultos. *Hylodes asper* tem um sistema de comunicação visual complexo, destacando-se a sinalização realizada com os membros posteriores ("foot-flagging"), que é a mais distintiva dentro do repertório de sinais visuais. Os borrifos d'água, produzidos pelas corredeiras e cachoeiras, criam uma umidade elevada e constante próximo aos riachos, reduzindo os riscos de dessecação, o que possibilita a atividade diurna de *H. asper.* Embora a intensidade do ruído ambiental seja similar à da vocalização de anúncio de *H. asper*, esta é espectralmente diferente do ruído produzido pelas corredeiras e cachoeiras. Assim, o ruído ambiental não parece representar uma fonte importante de interferência na comunicação acústica desta espécie. O ruído e a umidade elevada e constante gerados pelas corredeiras e cachoeiras, juntamente com a disponibilidade de luz, provavelmente favoreceram a evolução de colorações contrastantes e comunicação visual em *H. asper.* Machos de *H. asper* escavam tocas subaquáticas que provavelmente são usadas para proteger a desova contra predadores e prevenir que os ovos sejam carregados pela correnteza.

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